A FEN ON THE NORTHERN CALIFORNIA COAST

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Introduction

Sphagnum bogs are not common in California but are to be found in montane situations and, as a novelty, at elevations of less than 650 feet above sea level in drainage hollows on the sterile sands of the Blacklock soil series in the 'pygmy forest' area of Mendocino County. They have been unknown at sea level in this state. However, along the coast of the Pacific Ocean, in Oregon, Washington, British Columbia and Alaska, bogs among the sand-dunes are not uncommon. This paper reports the existance of a stand of sphagnum-containing aquatic and semi-aquatic vegetation six and a half miles north of Fort Bragg (Mendocino County), between Cleone and Inglenook (fig. 1). This appears to be the southernmost extant example of this kind of vegetation on the Pacific Coast and is better described as a fen than as a bog—and will be referred to in this paper as the Inglenook fen.

Fens have been studied most carefully in the British Isles (where they are especially extensive in eastern England) and it may, therefore, be most appropriate to turn to the late Sir Arthur Tansley's encyclopedic account of British vegetation for an explanation of the differences between marsh, fen and bog. Tansley (1939, p. 634) gives the title *marsh* to a soil vegetation type in which the soil is waterlogged, the summer water level being close to or conforming with, but not normally much above, the ground level, and in which the soil has an inorganic (mineral) basis. *Fen* is a corresponding type (whose vegetation is closely similar to that of a marsh) in which the soil is organic (peat) but may be alkaline, neutral or even somewhat acid in reaction. *Bog,* on the other hand, forms peat which is extremely acid and bears a radically different vegetation. Usually, the soil of a bog is very poor in exchangeable bases while a fen is relatively rich in them and, as a consequence, rather highly productive.

In fens, the soil may be pure peat or, if silting is a factor in the basin where the water accumulates, it may contain varying amounts of mineral matter. Often fens are clearly successional stages in hydroseres leading to a forest climax; the Inglenook fen appears to be of such a type and is surrounded by a woody *fen-carr* (cf. Tansley, 1939, p. 644).

For about ten miles along the coast north of Fort Bragg there are magnificent unstable sand-dunes. Sand which is brought to this stretch of the coast by ocean currents is carried onshore by tidal action and deposited. When dry, it is blown inland by the prevailing westerly winds. These sand-dunes are advancing over the lowest of a series of terraces (actually raised beaches) formed by a combination of ocean level changes and local tectonic movements. Gardner (1967) has described a series of these terraces at 100, 175, 300, 475 and 600 feet elevation. It is the lowest (and most seaward) of these which is presently being

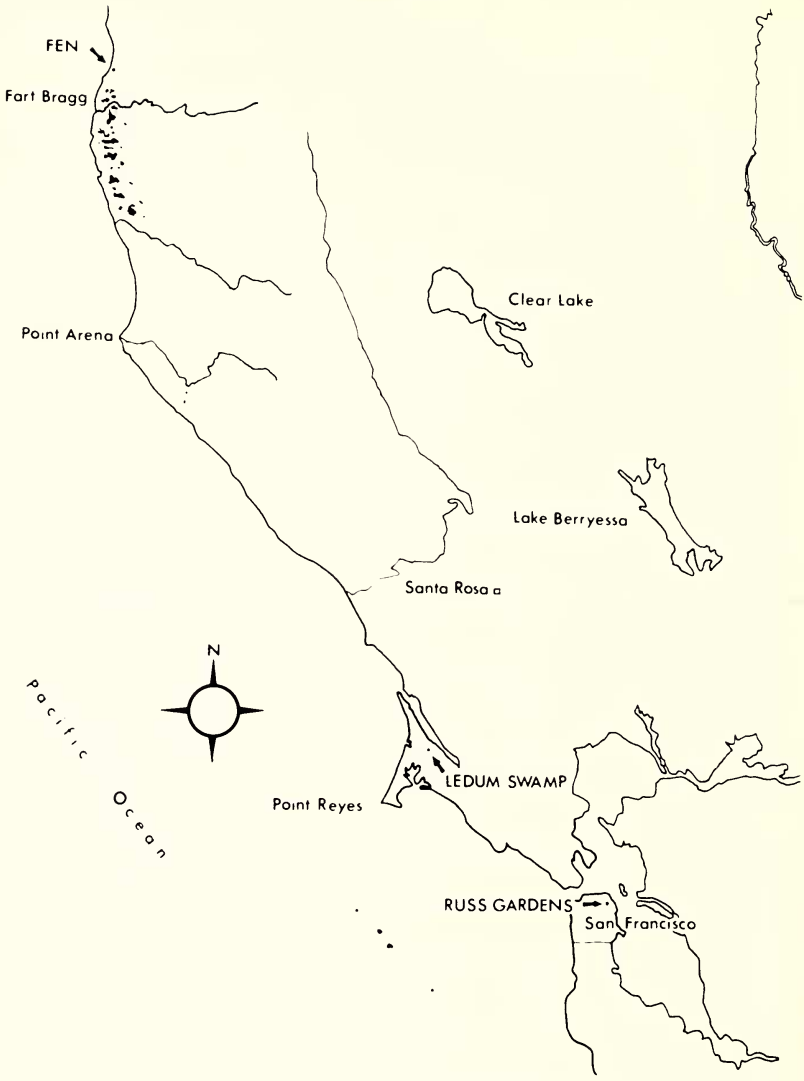

FIG. 1. Fen–locations in California: shaded areas around and south of Fort Bragg are the "pygmy forests."

invaded by the sand-dunes. It is largely covered with coastal prairie (Munz and Keck, 1949–50). The coniferous forests of the area are developed on the older and higher dune and terrace systems and contain mostly *Pinus muricata* D. Don, *Sequoia sempervirens* (D. Don) Endl. and *Pseudotsuga menziesii* (Mirb.) Franco. Streams draining toward the coast from these forested hills are impeded by the sand-dunes and this is how Inglenook Fen is formed.

Slightly farther south are the "pygmy forests" of *Pinus contorta* Dougl. var. *bolanderi* (Parl.) Vasey and *Cupressus pygmaea* (Lemmon) Sarg. (fig. 1). The soils of all the coniferous forests are podsolized and those of the pygmy forest represent an extreme in podsolization (Jenny, Arkley and Schultz, 1969). Although the streams draining from the forests into the Inglenook fen are too far north to carry drainage water from the "pygmy forests" and their associated bogs, they are distinctly acid in reaction. One such stream leads into the fen under State Route 1, 75 yards north of the junction with Little Valley Road, about 6 miles north of Fort Bragg. The pH of its water measured on July 10, 1966 (Beckmann pH meter, model N) was 4.9. During and after the winter rains the pH rises (e.g to 6.5 on April 12, 1969). On the other hand, the sand-dunes into which the stream flows are rich in shell-fragments. As a result, both the pH and the base status of the fen (which lies between the road and the dunes) may be expected to be raised by the material which slips down or is blown from the dunes into the fen and by the waters which drain from the dunes. A final barrier to the escape of water from among the dunes is posed by the "Ten Mile River Logging Road" of the Boise Cascade Company which runs from Fort Bragg to the Ten Mile River along the margin of the ocean. Although there is evidence of seepage and actual overflow beneath the road in one place, the impediment is a real one and the area around the "outlet" receives enough moisture to allow grass to grow and provide for limited cattle grazing. As a consequence of these physical and chemical features of the environment, a floristically rich and luxuriant vegetation (contrasting in dramatic fashion with the floristic poverty and apparently very low productivity of the true bogs of the "pygmy forest" are) is produced—the Inglenook fen.

My attention was called to the existence of this remarkable piece of vegetation by my interest in one angiosperm species which is an important constituent of it. *Menyanthes trifoliata* L., the Bog Bean (or Buck Bean), belongs to the family Menyanthaceae. It is of interest to students of reproductive biology by reason of the heterostyly of its flowers (Darwin, 1877; Baker, 1959). The species has a circum-boreal distribution and usually grows in acid waters; in northern Europe as well as in eastern and northern North America it occurs at sea-level as well as in the mountains, but passing southward in western North America the lowland part of the elevational range is supposedly lost. In California, its contemporary altitudinal range is given as 3,000 to 10,000 feet above sea-level by Jepson (1939). According to Mason (1957) it is restricted to the Sierra Nevada, while Munz (1959) reports its occurrence only at elevations of 3,000 to 10,500 feet (in Yellow Pine Forest to Subalpine Forest). Hewett (1964), in his account of the ecology of *M. trifoliata* for the 'Biological Flora of the British Isles', draws conclusions as to the limits for this species in western North America on the basis of the distribution given in Munz (1959).

Consequently, I was excited when shown by Wayne Roderick a specimen of this species which he had collected at sea level in Mendocino County. I was introduced to the owner of the property, R. R. Ross, who graciously gave me permission to make a study of the plants and their habitat.

Both long-styled and short-styled plants of *M. trifoliata* occur in the Inglenook fen, so an artificial introduction of the species from one of its well-known high-altitude stations becomes an unlikely explanation for this apparently unique occurrenec at sea level in California. As will be seen later, the naturalness of its occurrence is backed up by the floristic constitution of the vegetation here—an association of species which naturally accompanies *Menyanthes* in a series of boggy sitautions northward along the Pacific coast to Alaska but is otherwise unknown from California at the present day. Hansen (1943) records *M. trifoliata* from what appears to be the next fen northwards, five miles south of Bandon, Coos County, Oregon. Here again, drainage from land covered by pine trees *(Pinus contorta)* is impeded by actively moving sand-dunes. *M. trifoliata* also occurs in other coastal bogs and fens as far north as British Columbia and Alaska (cf. Rigg, 1922, 1925; Jones, 1936; Hanson and Churchill, 1961, p. 182; etc.).

Although no lowland occurrence of *M. trifoliata* in California is mentioned by Mason (1957), there is, in the University of California Herbarium *(UC),* in Berkeley, a specimen collected by him on 18 May, 1946 *(Mason 12771),* at this very site.

The occurrence near sea level of a species which is otherwise of higher altitude distribution in California recalls two other instances. Along the South Fork of the Eel River, near Pesula Road, in Humboldt County, Ichiro Fukuda has found a triploid plant of *Achlys triphylla* (Sm.) DC. growing among the usual tetraploid plants under the shade of the Coast Redwood *(Sequoia sempervirens).* A diploid form occurs at higher elevations, usually under Douglas Fir *(Pseutotsuga menziesii)* and the triploid is most reasonably explained as a relic hybrid from the days when the diploid grew at a lower altitude than that of its present stations (Fukuda, 1967). Similarly, A. P. Nelson (1962), investigating the genecology of *Prunella vulgaris* L. in California, concluded that some samples from the immediate vicinity of the South Fork of the Eel River (at Eagle Point, Humboldt County) also showed more affinity with montane races than is usually the case for plants growing at only 200 feet above sea level.

There is little doubt that there was a perceptible cooling of climate, during the glacial episodes of the Pleistocene epoch, far south of the limit of the ice sheets (Heusser, 1960; Axelrod, 1967). Unfortunately, the precise record for the northern California coast has still to be worked out. Thus, the pollen sequences in peat bogs studied by Heusser (1960), one of which was located two miles southeast of Fort Bragg in the pygmy

forest, begin only in the Late Postglacial, so that they show little divergence from contemporary pictures.

One conclusion of Heusser's, however, which may be important for our consideration is that there was an extensive marine transgression along the Pacific coast between 4,500 and 2,000 B.C., apparently due to a eustatic rise in sea level resulting from the melting of polar ice during the Hypsithermal (or Altithermal) period. According to H. Jenny (personal communication) the rise in sea level was probably of the order of ca 13 feet. The altitude of the fen at present is less than 40 feet above sea level and the open water (shown on the latest topographic map as "Sandhill Lake") is 24 feet above sea-level, but no data are yet available to show whether this eustatic change would have caused marine flooding in the fen because we know nothing of geologically recent isostatic changes which may have occurred in the area. Even if the fen did not exist in its present site, conditions for its occurrence may then have been favorable farther inland.

The direct influence of the raised temperatures of the Hypsithermal must also be taken into account. There is some evidence)Heusser, 1960; Axelrod, 1967) that the Bishop Pine *(Pinus muricata)* extended its range farther northward at this time (6,000–1,000 B.C.) and that Sitka Spruce *(Picea sitchensis)* has migrated southward since that time in response to a favorable increase in moisture. The present southernmost stand of Sitka Spruce is located between Mendocino and Fort Bragg. Consequently, it may be that the Inglenook fen is not more than 3 or 4 thousand years old, although, on the other hand, it (and its flora, in particular) may also have a California coastal history which reaches back to the Pleistocene.

If the *Menyanthes* population in the Inglenook fen should truly be a relic from a cooler climatic period in the past (persisting in its present locality because of the chill fogs which beset the Fort Bragg area, particularly during the summer months), it might be expected that traces of the same plant association would be discovered elsewhere. In fact, there is another lowland record of *M. trifoliata,* from San Francisco, where it flourished in a "marsh" until it became extinct in 1859 (Behr, 1888). The circumstances of this occurrence will be referred to later.

Structure and Composition of the Inglenook Fen

The Inglenook fen shows a well-marked zonation which is indicated roughly on the sketch-map (fig. 2). The following zones may be distinguished:

Open water (a) with fringing emergent vegetation
Fen proper (b) almost pure *Carex* and *Heleocharis* tussocks
(c) *Calamgrostis*/Cyperaceae/*Menyanthes* fen with *Ledum, Sphagnum,* etc.
(d) Fen carr

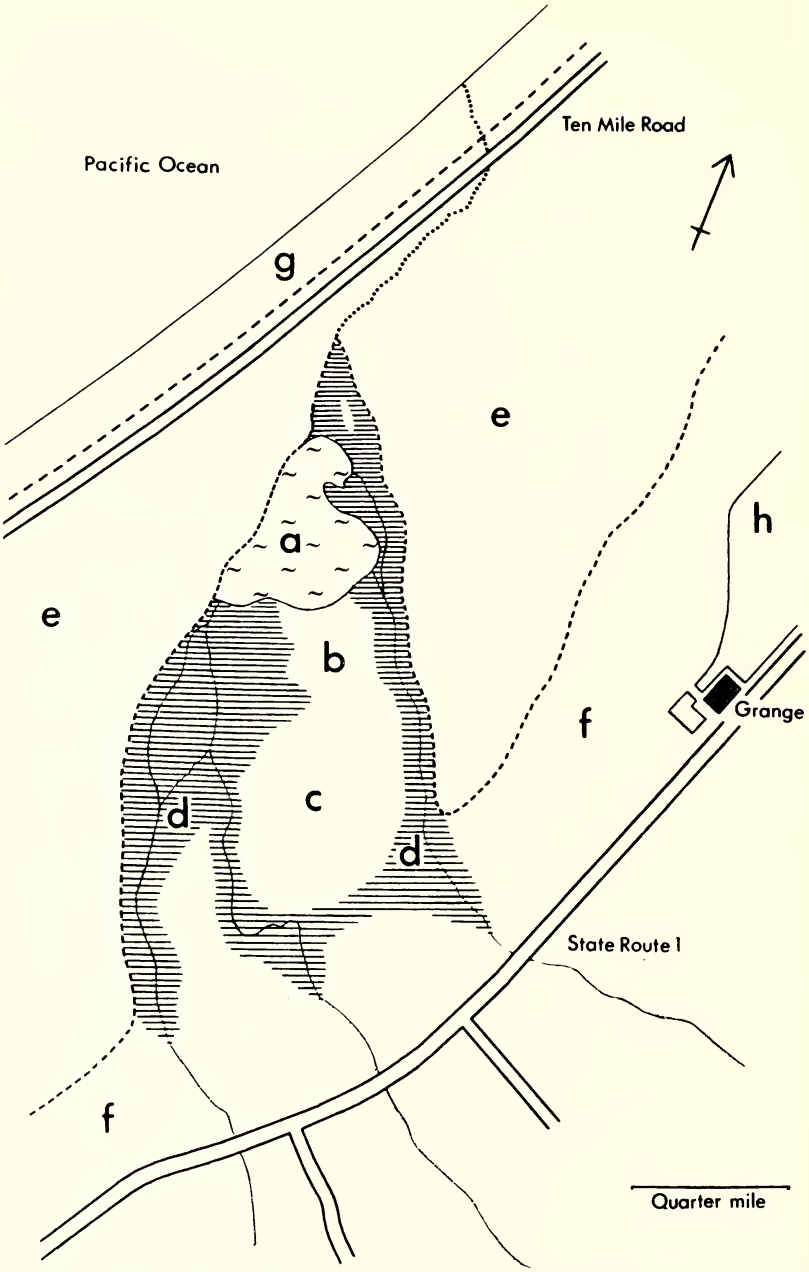

FIG. 2. Sketch map of the Inglenook Fen and surroundings: a = open water; b = Cyperaceae dominated fen; c = Calamagrostis-Cyperaceae-Menyanthes fen; d = fen carr; e = sand dunes; f = coastal prairie; g = strand; h = Eucalyptus plantation.

The fen as a whole is bounded by the sand-dunes (e) which, of course, have a quite distinct flora and, at its inland limits, merges with the coastal prairie (f) of the 100 foot raised beach. The four major zones within the fen presumably represent successive stages in a hydrosere leading from fresh water which is too deep for rooted phanerogamic vegetation to a wet forest-type which is rather stable and might not give way to pine forest until some further raising of the land occurs.

Table 1A shows the results of analyses of water samples and, for comparison, a water extract of the sand-dune immediately adjacent to the fen. The influence of drainage and slippage from the dune in raising the pH of the pond is clear, as is the effect of peat formation in depressing it in the fen. The dunes are rich in calcium and contribute this to the fen while the sodium mostly comes from the inflow creek (and probably also from spray blown in from the sea). The calcium content of the water is high enough to supply plant needs and counteract unfavorable effects of high concentrations of sodium (H. Jenny, personal communication).

Table 1A. Water Samples and Water Extracts (me/liter).

	pH	Na	K	Ca	Mg	Totals
Water from inflow creek	6.5	.66	.03	.40	.42	1.51
Water from auger hole (fen)	5.2	.97	.12	.20	.23	1.52
Water (surface) from Nuphar zone	5.6	.68	.02	.56	.25	1.51
Water from pond (west end)	7.0	.91	.03	.72	.27	1.93
Water extract of sand-dune (4 grms. in 250 ml.)	8.1	.10	.02	.93	.24	1.23

In Table 1B the acidity of the fen peat along with the relatively high base status of the samples is indicated. By comparison bog and sandy soil samples from the Blacklock soil series in the "pygmy forest" have even lower pH values and lower base status (A. E. Salem, unpub., and Jenny, et al., 1969).

Table 1B. Soil Samples—Exchangeable Bases (me/100 g. oven-dry material).

	pH	Na	K	Ca	Mg	Totals
Cyperaceae fen	4.5–4.8	6.6	5.1	18.2	13.6	43.5
Calam./Sphagnum fen	4.6	5.1	2.2	18.8	12.9	39.0
Fen carr (Menyanthes)	4.6–5.1	6.2	6.2	17.2	16.1	45.7
Fen carr	4.2	6.0	9.2	23.0	18.5	56.7

The floristic composition of the vegetational zones (table 2) is given without any claim that the lists are complete. All aspects of the ecology of this fen should be studied in appropriate detail in the future. When this is done, subdivision of the zones in the fen will certainly be possible. For example, the western part of the fen (toward the open water) consists of almost pure *Carex* and *Heleocharis* tussocks, while the greatest floristic diversity occurs in the central and eastern part of the fen. Topo-

Table 2. Floristic Composition of Zones in Inglenook Fen

	Zone 1 Open water	Zone 2 Fringing emergents	Zone 3 Fen	Zone 4 Fen Carr
Nuphar polysepalum Engelm.	+	+	+	
Equisetum hyemale L. var. robustum (A. Br.) A. A. Eat.		+		
Potentilla palustris (L.) Scop.		+	+	+
Cicuta douglasii (DC.) Coult. & Rose		+	+	
Oenanthe sarmentosa Presl		+	+	
Scirpus acutus Muhl.		+		
Typha latifolia L.		+	+	
Sphagnum sp.			+	
Calliergonella cuspidatum (L.) Loesk.			+	
Blechnum spicant (L.) Roth.			+	+
Hypericum anagalloides Cham. & Schlecht.			+	+
Nasturtium officinale R. Br.			+	
Ledum glandulosum Nutt. spp. columbianum (Piper) C. L. Hitchc.			+	
Gentiana sceptrum Griseb.			+	
Menyanthes trifoliata L.			+	+
Mimulus guttatus Fisch.			+	+
Myrica californica Cham. & Schlecht.			+	+
Epilobium adenocaulon Hausskn. var. parishii (Trel.) Munz			+	
E. watsonii Barb. var. franciscanum (Barb.) Jeps.			+	
Hydrocotyle ranunculoides L. f.			+	
Campanula californica (Kell.) Heller			+	
Veratrum fimbriatum Gray			+	
Lysichiton americanum Hult. & St. John.			+	+
Sisyrinchium californicum (Kerr) Dry.			+	
Habenaria dilatata (Pursh.) Hook. var. leucostachys (Lindl.) Ames			+	
Juncus effusus L. var. pacificus Fern. & Wieg.			+	+
J. effusus L. var. brunneus Engelm.			+	+
J. bolanderi Engelm.			+	
J. lesueurii Bol.			+	
J. phaeocephalus Engelm.			+	
J. ensifolius Wikstr.			+	+
Heleocharis acicularis (L.) R. & S.			+	
Carex vicaria Bailey			+	+
C. obnupta Bailey			+	+
Glyceria occidentalis (Piper) J. C. Nels.			+	
Calamagrostis nutkaensis (Presl.) Steud.			+	
Athyrium filix-foemina (L.) Roth. var. sitchense Rupr.				+
Scrophularia californica Cham. & Schlecht.				+
Collinsia corymbosa Herder				+
Veronica americana (Raf.) Schw.				+
Stachys stricta Greene				+
Potentilla egedei Worms. var. grandis (Rydb.) J. T. Howell				+
Rubus vitifolius Cham. & Schlecht.				+
Lotus aboriginum Jeps.				+

TABLE 2. *Continued.*

	Zone 1	Zone 2	Zone 3	Zone 4
Vicia americana Muhl. ssp. oregana (Nutt.) Abrams				+
V. gigantea Hook.				+
Alnus oregona Nutt.				+
Salix piperi Bebb.				+
S. sitchensis Sanson				+
S. coulteri Onderss.				+
Galium trifidum L. var. subbiflorum Wieg.				+
Lonicera involucrata (Rich.) Banks var. ledebourii (Esch.) Zabel				+
Baccharis douglasii DC.				+
Erechtites prenanthoides (A. Rich.) DC.				+
Smilacina stellata (L.) var. sessilifolia (Baker) Hend.				+
Polypogon monspeliensis (L.) Desf.				+

graphic diversity within the fen is provided by the tussocks of Cyperaceae and, especially, by the large tussocks of *Calamagrostis* and the build-up of material around the bases of the *Ledum* and *Myrica* bushes. Thus, *Menyanthes* and *Epilobium adenocaulon* can grow in the same zone in hollows and on tussocks, respectively.

The soils of the fen are by no means unrelieved peat; sand and mineral particles of smaller size occur in all zones. The mineral content predominates in the soil beneath the open water but decreases in proportion through the fen (where the loss on ignition averages about 50% of the dry weight of the soil) to the fen carr (where the loss on ignition reaches 77% in the surface litter and 78% in the subsurface peat). In the fen, *Sphagnum* peat appears to be accumulating patchily and much of the rest of the peat is derived from flowering plant remains.

Because the water and the peat in the fen have an acid reaction, the presence of such well-known "calcifuges" as *Sphagnum* spp., *Potentilla palustris, Blechnum spicant* and *Myrica californica* is not surprising. On the other hand, the reasonably high base status is indicated by the presence of such species as *Nasturtium officinale, Habenaria dilatata* and *Lysichiton americanum*. A notable absentee (present in the much shorter floristic lists from the acid, base-deficient bogs of the "pygmy forest" not far away) is the sundew, *Drosera rotundifolia*. Good descriptions of these "pygmy forest" bogs can be found in Rigg (1933) and McMillan (1956).

RELATION OF INGLENOOK FEN TO OTHER "BOGS" AND "MARSHES"

Table 3 shows species which are in common between the Inglenook fen and a number of coastal "bogs" ranging from Alaska southwards to

Table 3. Species in Common Between a Number of Coastal "Bogs" and "Fens" on the Pacific Coast of North America

	1	2	3	4	5	6	7
	Palmer, Alaska (incomplete)	Victoria, B.C.	Olympic Penin. Wash.	Bandon, Ore.	Inglenook, Calif.	Ledum Swamp (Point Reyes) Calif.	San Francisco, Calif. (incomplete)
Nuphar polysepalum	+	+	+	+	+		
Potentilla palustris	+	+	+	+	+		
Oenanthe sarmentosa		+			+	+	(+)
Sphagnum sp.	+	+		+	+		
Calliergonella cuspidatum		+			+		
Blechnum spicant					+	+	
Hypericum anagalloides					+	+	
Ledum spp.		+		+	+	+	
Gentiana sceptrum, etc.		+		+	+		
Menyanthes trifoliata	+	+	+	+	+		+
Mimulus guttatus					+	+	
Myrica spp.		+		+	+	+	
Lysichiton americanum				+	+		
Sisyrinchium californicum					+	+	
Habenaria dilatata var. leucostachys					+	+	+
Calamagrostis nutkaensis					+	+	
Athyrium filix-foemina					+	+	+
Alnus oregona		+		+	+		
Campanula californica					+	+	
Carex obnupta					+	+	
Heleocharis acicularis				+	+		

1. Hanson and Churchill (1961); 2. Rigg (1922, 1925); 3. Jones (1936); 4. Hansen (1943); 5. See Table 2; 6. Howell (1949); 7. Behr (1891), etc.

southern Oregon. In addition, the last column in the table indicates that some of these species were also present in the extensive "marsh" in San Francisco which Behr (1891) describes as having been destroyed by the growth in the city in the second half of the nineteenth century.

The San Francisco "marsh," which contained black, peaty soil according to Kellogg (cited by Brandegee, 1892), was adjacent to a pleasure resort called the Russ Gardens after the family who owned it. This was situated on the south corner of the intersection of Sixth and Harrison Streets (Eastwood, 1945). Behr (1891) describes the situation thus (Behr's punctuation is preserved): "Near the formerly well known Russ Gardens there were extensive marshes abounding especially about their borders in interesting plants. Here grew the large flowered dogwood *(Cornus Nuttallii),* the buckbean *(Menyanthes trifoliata), Epipactis gigantea,* the delightfully fragrant *Habenaria leucostachys,* and *Eriophorum gracile.* In the same vicinity I found in a single locality five

specimens of *Botrychium ternatum;* and the Lady-fern *(Asplenium filix-foemina),* grew luxuriantly, often forming root-stocks two feet high, simulating tree ferns." According to Eastwood (1945), Behr also found *Hippuris vulgaris* and Brandegee (1892) notes that Behr found *Cordylanthus maritimus* (under the name *Chloropyron palustre)* at this place.

No trace remains now of this, which must have been the southernmost representative of the coastal bog or fen formation along the Pacific Coast of North America. However, it is possible that an impoverished fragment of another example remains about 30 miles north of San Francisco, at the landward end of Point Reyes Peninsula. This is the well-known "Ledum Swamp" where acid waters draining from the quartz-diorite Inverness Ridge (covered with *Pinus muricata* and a podsolized soil) are impeded by nutrient-rich hills on the Peninsula. The next to last column in Table 2 contains a list of the species (from Howell, 1949) still occurring in Ledum Swamp which are also to be found in the Inglenook fen.

Only Inglenook fen now remains in California to represent this soil-vegetation type adequately, but it is a magnificent example. Because of its floristic richness and the completeness of its zonation and because it is the southernmost example of its kind, it is to be hoped that this fen can be preserved intact for study through the years to come. The area is also of anthropological interest, because it was here that the Coast Yuki Indians lived. This physically and linguistically isolated people and their artifacts are in need of further study (cf. Barrett, 1908; Thomsen and Heizer, 1964).

In this preliminary study of the Inglenook fen, I was greatly assisted by a Research Grant from the National Science Foundation (G-21821). Nothing would have been possible without the kind permission of the owners of the land, Mr. and Mrs. Ross. Robert Frenkel, Arthur Weston, Ann Mendershausen and Diana Myles also helped in collecting the field data. Hans Jenny kindly arranged for and A. E. Salem carried out the soil and water analyses.

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NOTES AND NEWS

Pleurophycus gardneri Setchell & Saunders, a new alga for Northern California.—The Laminariales have received considerable attention recently with Druehl's publications (Can. J. Bot. 46:539–547. 1968; Phycologia 9:237–247. 1970) on their distribution along the west coast of North America. In general, the Northern California Coast from Bodega Head to the Oregon border has received very little attention with the exception of Dawson's study (Marine Algae in the vicinity of Humboldt State College, Biology Department, Humboldt State College, Arcata, Ca., 1965). On 12 July 1971, collections of algae were made in the intertidal zone at Fort Bragg (39° 27′N, 123° 47′W) during —1.0 foot tide. One of the specimens has been deposited in the herbarium at Hopkins Marine Station. Other voucher specimens have been deposited in the Sonoma State College herbarium. At this locality, *Pleurophycus gardneri* Setchell & Saunders, heretofore known only north of Coos Bay, Oregon (43° 25′N, 124° 20′W) was collected from a large population on rocks at —1.5 foot tide level in a tide pool area. A single specimen was also collected by the author in October, 1970, from the drift at Salt Point (38° 36′N, 123° 21′W).—Chris K. Kjeldsen, Department of Biology, Sonoma State College, Rohnert Park, California 94928.